Does foliar nutrient resorption regulate the coupled relationship between nitrogen and phosphorus in plant leaves in response to nitrogen deposition?

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HIGHLIGHTS

- Global NRE and PRE under natural condition are run by biotic and abiotic factors.
- N addition decreased the NRE but slightly affected the PRE on a global scale.
- Nutrient-limited conditions regulated response of nutrient resorption to N addition.
- Different response of N and P relationship to N addition in green and senesced leaves
- Nutrient resorption regulated N and P relationships in leaves response to N addition.

GRAPHICAL ABSTRACT
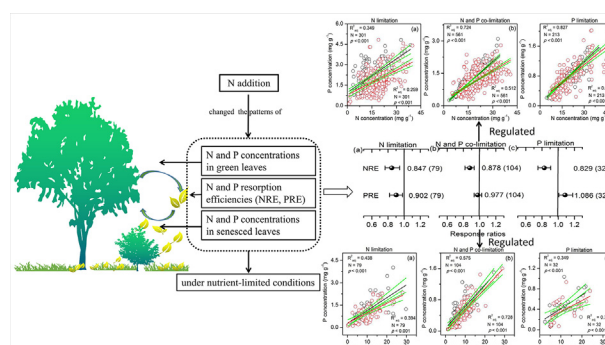
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ABSTRACT

Nutrient resorption from senescing leaves is an important process of internal nutrient cycling in plants, but the patterns of nutrient resorption and the coupled relationship between nitrogen (N) and phosphorus (P) in plant leaves as affected by N deposition remain unclear. We analysed the effects of N addition on the nutrient resorption and coupled relationship between N and P in plant leaves under different nutrient-limited conditions based on a global meta-analysis. Globally, the mean N resorption efficiency (NRE) and P resorption efficiency (PRE) under natural conditions were 47.4% and 53.6%, respectively, which were significantly regulated by geographical and climatic factors as well as plant characteristics. Furthermore, N addition significantly decreased the NRE by 13.3% but slightly affected the PRE on a global scale, and N addition rates and latitude directly and negatively affected the effects of N addition on NRE. Specifically, N addition significantly decreased the NRE under all nutrient-limited conditions, while it had negative, positive, and neutral effects on the PRE under N-limited, P-limited, and N and P-co-limited conditions, respectively. Moreover, the relationships between N and P in green and senesced leaves were tightly coupled under different nutrient-limited conditions in natural ecosystems. However, N addition significantly weakened the relationships between N and P concentrations in green leaves but slightly affected the relationship in senesced leaves, which were mainly modulated by the effects of N addition on nutrient resorption efficiency, especially NRE. These results highlight that nutrient-limited conditions determine the response of nutrient resorption to N deposition and emphasize the effect of nutrient resorption regulation on the coupling of N and P responses to N enrichment. The findings are important for understanding

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plant nutrient use strategies and the mechanisms underlying the stoichiometric coupling of N and P in response to climate change, and can be used in global biogeochemical models.

1. Introduction

Nutrient resorption of senesced organs is an important strategy for plants to conserve and reuse nutrients, especially nitrogen (N) and phosphorus (P) (Aerts, 1996; Chen et al., 2015; Killingbeck, 1996; Kobe et al., 2005; Vergutz et al., 2012), which can improve plant nutrient use efficiency and reduce plant growth dependence on soil nutrients (Aerts and Chapin III, 1999; Wright and Cannon, 2001). Therefore, nutrient resorption plays a paramount role in guaranteeing plant growth and reproduction and maintaining productivity and nutrient cycles in global ecosystems (Yan et al., 2015; Yuan and Chen, 2009); in addition, it provides a key scientific basis for understanding how plants adapt to climate change (e.g., N deposition) (Mayor et al., 2014; Rejmánková and Snyder, 2008; Wang et al., 2014). It is well known that increasing N deposition alters the plant nutrient regime and elemental balance (Peñuelas et al., 2013; Peñuelas et al., 2015), and has far-reaching effects on the structure, function and nutrient cycling of ecosystems (An et al., 2011; Deng et al., 2017; Li et al., 2016; Niu et al., 2016). However, the pattern of the effects of N deposition effects on nutrient resorption in global ecosystems has not been well characterized.

Previous studies have demonstrated that, on a global scale, nutrient resorption is modulated by biotic factors such as plant growth type (Yuan and Chen, 2015a), species specificity (Mayor et al., 2014; Wang et al., 2014) and leaf characteristics (Chen et al., 2015; Heerwaarden et al., 2003; Huang et al., 2007; Kobe et al., 2005) and abiotic factors including climatic factors (Yuan and Chen, 2009), geography factors (Yuan and Chen, 2009) and soil nutrient content (Aerts and Chapin III, 1999; Vergutz et al., 2012). Recently, many experimental studies have focused on the effects of N addition on nutrient resorption (Lü and Han, 2010; Lü et al., 2016; Mayor et al., 2014; Wang et al., 2014; Yan et al., 2015) and have found that N addition significantly decreases N resorption efficiency (NRE) (Chen et al., 2015; Mayor et al., 2014; Wang et al., 2014). In contrast, the responses of P resorption efficiency (PRE) to N addition have varied greatly among studies, showing positive (Wang et al., 2014), negative (Lü et al., 2016) and neutral (Lü et al., 2013) effects. These uncertainties may be attributed to different patterns of nutrient limitation (such as N-limited, N and P-co-limited and P-limited conditions). For instance, N addition can increase soil N availability and alleviate the limitation of plant growth by N (Li et al., 2016; You et al., 2017), whereas excessive N addition can stimulate phosphate enzyme activities and promote soil P availability (Deng et al., 2016; Fujita and Wassen, 2010; Marklein and Houlton, 2012), with these effects ultimately altering the patterns of nutrient resorption in plants. However, little information has been available on how different nutrient-limited conditions regulate the responses of NRE and PRE to N addition on a global scale.

N and P are two essential nutritional elements that couple from molecular to global scales to control biological growth, respiration, and decomposition as well as the biochemical cycles in ecosystems (Finzi et al., 2011; Peñuelas et al., 2015). Many comprehensive analyses have discussed the relationship between N and P in different organs, populations, plant functional groups and ecosystems (He et al., 2008; Reich and Oleksyn, 2004; Yuan et al., 2011). However, few studies have assessed the relationship between N and P in green and senesced leaves under different nutrient-limited conditions. Meanwhile, N addition can significantly affect the N and P concentrations in green and senesced leaves as well as the pattern of nutrient resorption (Lü et al., 2016; Mayor et al., 2014; Yan et al., 2015; Yuan and Chen, 2015a). In addition, previous studies have shown that increasing N deposition has aggravated P limitation

of plant growth (Li et al., 2016) and altered the limitation of nutrient patterns in ecosystems (Elser et al., 2007; Harpole et al., 2011; Vitousek et al., 2010). However, as an important process of element transfer between green leaves and senesced leaves, the role of nutrient resorption during leaf senescence in regulating the relationship between N and P in response to N addition under different nutrient-limited conditions remains unclear.

Here, we performed a global meta-analysis of studies across multiple ecosystems to specifically understand how nutrient resorption controls the response of the relationship between N and P in green and senesced leaves to N addition under different nutrient-limited conditions. Following previous analyses of the effects of N addition on nutrient resorption, and the N and P concentrations in green and senesced leaves (Kozovits et al., 2007; Mayor et al., 2014; Wang et al., 2014; Yuan and Chen, 2015a), we predicted that nutrient-limited conditions determine the response of nutrient resorption to N addition, and that the NRE and PRE correspondingly regulate the relationship of N and P to N enrichment. To test this hypothesis, this study addressed the following questions: (1) What is the average NRE and PRE under N addition on a global scale, and do different nutrient-limited conditions produce significantly different NRE and PRE values? (2) Is there a significant relationship between N and P in green and senesced leaves under different nutrient-limited conditions? (3) How does N addition affect the N and P relationship in green and senesced leaves, and do the NRE and PRE regulate this relationship in response to N enrichment?

2. Materials and methods

2.1. Data compilation

We used Web of Science, Google Scholar and China National Knowledge to collect data from primary studies published before September 2017. The fundamental purpose of the data collection was to compile a database that included the responses of NRE, PRE and N and P concentrations in green and senesced leaves to N enrichment. Thus, the search terms were "N addition", "N deposition", "N fertilization", "nutrient resorption efficiency", "foliar N and P concentrations", "senesced leaves N and P concentrations" and "foliar stoichiometry", and the following criteria were used to minimize the bias of the publications and select appropriate case studies. (1) The data had to be derived from experimental studies that explored the influence of N deposition on the target variables, and the effects of fertilization management on plant nutrients were excluded. (2) At least one of the target indicators was measured, and the N and P concentrations in green leaves were included or calculated. (3) The data had to be derived from mature leaves or fresh litter leaves of dominant plants and only included the data at the individual level, while community-level data were excluded. (4) For multifactorial studies, only control and N addition treatments were included, and other treatments and interacting effects were not selected. (5) The data from control and N addition treatments were derived under the same conditions, and the duration of N addition was not less than one year. Finally, (6) if target variables from the same field observation experiment were published in different journal articles, we only used the average values for the analysis. In addition, to better understand and analyse the data, we also collected the N addition rates, geographic factors (including altitude (m), latitude (°) and longitude (°)) (Fig. S1 in the Supporting Information) and climatic factors (i.e., mean annual temperature (MAT, °C) and mean annual precipitation (MAP, mm)) (Table S3 in the Supporting Information). We used the Get Data Graph

Digitizer (version 2.24, Russian Federation) to extract the data from the graphs or tables of published articles. Furthermore, we also followed Moher et al. (2009) and created a flow diagram to detail the data collection process in this study (Fig. 1).

It is generally believed that terrestrial ecosystems are mainly limited by N (Lebauer and Treseder, 2008), but evidence has increasingly indicated that ecosystems may gradually become limited by both N and P as a result of increasing anthropogenic N and P addition to the biosphere and continual disruption of the N and P balance (Harpole et al., 2011; Li et al., 2016; Vitousek et al., 2010). In addition, previous studies have demonstrated that the N to P ratios in the mature leaves of dominant plants can determine the productivity of the community (Grime, 1998; Tessier and Raynal, 2003), and these ratios have been widely applied to diagnose nutrient limitation of plant growth (Güsewell et al., 2003; Güsewell and Koerselman, 2002; Killingbeck, 1996; Rejmánková, 2005; Xu et al., 2017). Therefore, to understand how nutrient-limited conditions influence the response of nutrient resorption to N addition and the role of nutrient resorption in regulating the relationship between N and P in green and senesced leaves in response to N enrichment in this study, we selected the threshold foliar N to P ratio values of 10 and 20, respectively (from the control groups), to classify the collected plants into N-limited, N and P-co-limited and P-limited plants. For example, based on previous studies (Güsewell et al., 2003; Güsewell and Koerselman, 2002), when the N to P ratios of the mature leaves of dominant species were less than 10, the plants were categorized as N-limited; when the ratios were greater than 20, the plants were categorized as P-limited; and when the ratios were between 10 and 20, the plants were categorized as N and P-co-limited.

2.2. Meta-analysis

We followed previous studies (Li et al., 2016; Yue et al., 2017; Yue et al., 2016) and used a meta-analysis approach to analyse the data. The response ratio (RR) was used to investigate the effects of N addition on each target variable, and which was calculated as follows: $\ln RR = \ln (Xe/Xc)$, where Xe stands for the treatment mean, and Xc stands for the control mean. The variance of each unnatural log of RR was quantified by the standard deviation of each independent variable. Then, we selected the meta-analytical software Meta-win 2.1 (Sinauer Associates, Inc. Sunderland, MA, USA) to conduct mixed modelling and calculate the weighted RR and the 95% confidence interval (95% CI). When the bounds of the 95% CI were larger or smaller than one, the weighted N addition RR was considered significantly positive or negative at $p < 0.05$, and if the bounds of the 95% CI overlapped one, the RR of the target variable was insignificant. The calculation formulas (such as the variance, weighted RR and 95% CI) used in this calculation method have been described in detail in previous studies (Li et al., 2016; Yue et al., 2017). To evaluate how the nutrient-limited conditions regulated the effects of N addition on the independent variable, we used the mixed models to compare the heterogeneity within (Qwithin) and the heterogeneity between (Qbetween) to investigate the significance of the categorical variable. If the 95% CI of the subgroups did not overlap, the mean of the weighted RR of the subgroups was significantly different.

2.3. Sensitivity analysis and publication bias

The sensitivity analysis was used to investigate the effects of each N addition treatment from each primary study on the individual
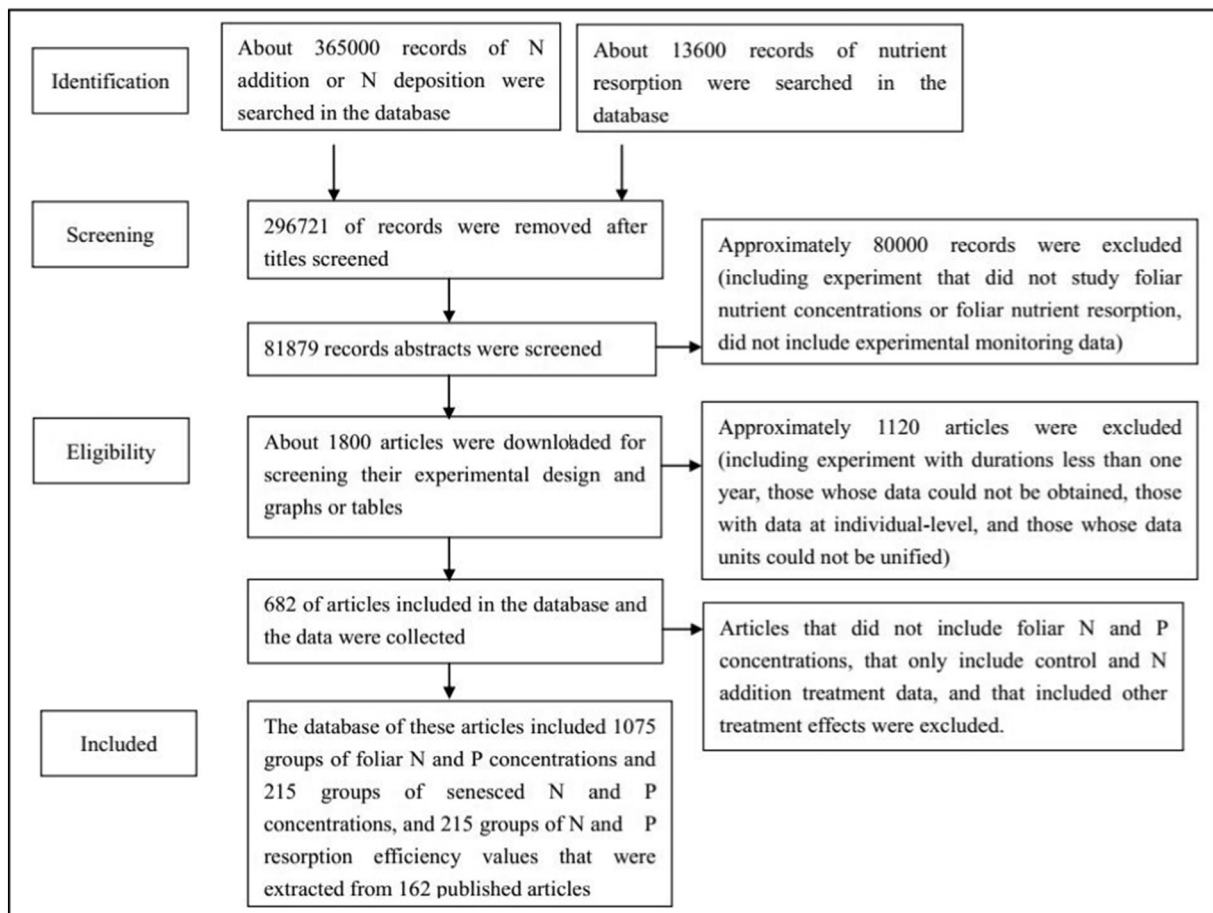

Fig. 1. Flow diagram of introduce the data selection process in this study.

observations (Koricheva and Gurevitch, 2014). Based on a previous study (Hedges et al., 1999), we conducted a mixed model analysis and used the weighted RR to estimate the effects of the variable effects; and a random selection of the effects of N addition on NRE and PRE from the primary study was used to repeat the analysis (You et al., 2017; Yue et al., 2017). The weighted RR results indicate that reducing the number of sample observation did not change the results of this study (Fig. S2 in the Supporting Information). Moreover, the publication bias was estimated by the Gaussian function (Fig. S3 in the Supporting Information), and the frequency distributions of all the RR values of the target variables followed a normal distribution, indicating an absence of publication bias in our study.

2.4. Statistical analysis

If the observation variable did not meet the normal distribution and homoscedasticty of error assumptions, then the data were log-transformed before analysis. To understand the distribution of and variability in the NRE and PRE, we performed a descriptive statistical analysis in which the curve was fitted by a Gaussian function. In addition, when the data were under different nutrient-limited conditions, we performed a regression analysis to examine the relationship between N and P in green and senesced leaves under natural conditions (the control treatment) and N addition. To minimize regression bias, we used the adjusted coefficient of determination (R^2_{adj}) to show the degree of fit. Moreover, to quantify the effects of N addition on the relationship between N and P concentrations in green and senesced leaves, we used general linear models (univariate covariance analysis) to compare the coefficients and intercepts of equations for N and P concentrations under natural conditions with those of equations under N addition. SPSS software (SPSS 17.0 for Windows; SPSS Inc., Chicago, IL, USA) was used for regression analysis and general linear models, and the graphs were constructed using Origin (version 8.0).

We used the path analysis to quantify the relationships between multiple variables and evaluate how climate (MAP and MAT) and geography (latitude, longitude and altitude) factors and the experimental parameters (study durations and N addition rates) directly and indirectly affect the nutrient resorption efficiency under natural conditions or regulate the response of nutrient resorption efficiency to N addition. According to previous studies of the relationship between the environment and nutrient resorption efficiency (Li et al., 2016; Yuan and Chen, 2009, 2015a), we created a model to predict causal relationships among multiple variables (Fig. S4 in the Supporting Information). We stepwise removed the nonsignificant paths from the model, which did not significantly increase the degrees of freedom. Based on previous studies (Durán et al., 2015; Yue et al., 2018), the χ^2-test, Bentler-Bonett normed fit index (NFI), Bentler's comparative fit index (CFI), and the root square mean error of approximation (RMSEA) were used to test the goodness-of-fit of the models. The path analysis was performed with AMOS version 23.0.

3. Results

3.1. Effects of N addition on nutrient resorption efficiency and the N and P concentrations in senesced leaves

The change in NRE and PRE varied greatly among the observations, and a slightly skewed normal distribution was observed (Fig. 2). In all considered studies, the global averages of NRE and PRE averages under natural conditions were 47.4 % and 53.6 %, respectively, and the coefficients of variation were high at 37.9% and 35.7%, respectively (Fig. 2a, b). In addition, the average NRE and PRE values under N addition on a global scale were 42.3% and 52.2%, respectively, and large coefficients of variation of 44.9 % and 39.9 %, respectively (Fig. 2c, d), were observed. Thus, across all studies on a global scale, N addition significantly decreased the NRE by 13.3 % but did not clearly affect the PRE

(Fig. 3a). When the global data were subdivided based on N limitation, N and P-co-limitation and P limitation, we found that N addition significantly decreased the NRE under all nutrient-limited conditions (15.3%, 12.2%, and 17.1%, respectively, Fig. 3b, c, d). However, the effects of N addition on the PRE were different under nutrient-limited conditions, and negative (9.8 %), positive (8.6%), and neutral effects on PRE were found under N limitation, P limitation, and N and P-co-limitation (Fig. 3b, c, d). Meanwhile, the magnitude of the effect of N addition on NRE under different nutrient-limited conditions was relatively greater than that on PRE (Fig. 3). Notably, the effects of N addition on NRE did not differ significantly under different nutrient-limited conditions, but the effect of N addition on PRE varied significantly (Table 1).

On a global scale, we also found that N addition significantly increased the N concentration in senesced leaves by 22.5 % but did not significantly affect the P concentrations of senesced leaves (Fig. 3a). Additionally, the effects of N addition on the N concentration of senesced leaves varied greatly among nutrient-limited conditions (Table 1). N addition had positive effects on N concentrations in senesced leaves under N limitation (32.7 %), N and P-co-limitation (22.3 %), and P limitation (20.4 %) (each with $p < 0.001$, Fig. 3b, c, d). In contrast, N addition did not affect P concentrations in senesced leaves under each nutrient-limited condition (each with $p > 0.05$, Fig. 3b, c, d).

3.2. Factors influencing nutrient resorption efficiency and the effects of N addition

Nutrient resorption efficiency (NRE and PRE) under natural conditions was influenced by a combination of climate (MAP and MAT) (Fig. 4a, b), geography (latitude, longitude and altitude) (Fig. 4a, b) and plant growth types (Fig. S5 in the Supporting Information). For example, PRE had the largest positive prediction for variation in NRE under natural conditions (Fig. 4a). In addition, NRE was directly and positively influenced by altitude, MAP and PRE, but directly and negatively influenced by MAT (Fig. 4a). Similarly, NRE had the largest positive prediction for variation in PRE (Fig. 4b). MAT and NRE had significant direct and positive effects on PRE, whereas longitude and MAP directly and negatively affected PRE under natural conditions (Fig. 4b). However, when the moderator variables that regulated the response of nutrient resorption efficiency to N addition were considered, N addition rates was mainly determined the effects of N addition on NRE (Fig. 4c). The response of NRE to N addition was directly and negatively influenced by N addition rates and latitude (Fig. 4c). Moreover, the effect of N addition on PRE was primarily regulated by MAT, and MAP directly and negatively affected the response of PRE to N addition (Fig. 4d). Additionally, we also found that the effects of N addition on nutrient resorption efficiency can be modulated by plant growth types (Table S2 in the Supporting Information).

3.3. Effects of N addition on the relationship between N and P concentrations in green and senesced leaves under different nutrient-limited conditions

Across the control and N addition treatments, N and P concentrations were positively correlated in both green and senesced leaves under different nutrient-limited conditions (all $p < 0.001$, Table S1 in the Supporting Information). In the control treatments, the P concentrations in green leaves significantly increased under all nutrient-limited conditions as the green leaves N concentrations increased, and the R^2_{adj} values were 0.349 under N limitation, 0.724 under N and P-co-limitation, and 0.827 under P limitation (all $p < 0.001$, Fig. 5a, b, c). In the N addition treatments, the N and P concentrations in green leaves were also significantly positively correlated, with R^2_{adj} values of 0.259 under N limitation, 0.512 under N and P-co-limitation, and 0.603 under P limitation (all $p < 0.001$, Fig. 5a, b, c). Notably, the R^2_{adj} values of the relationships between N and P concentrations in green leaves in the N addition treatments under all nutrient-limited conditions were
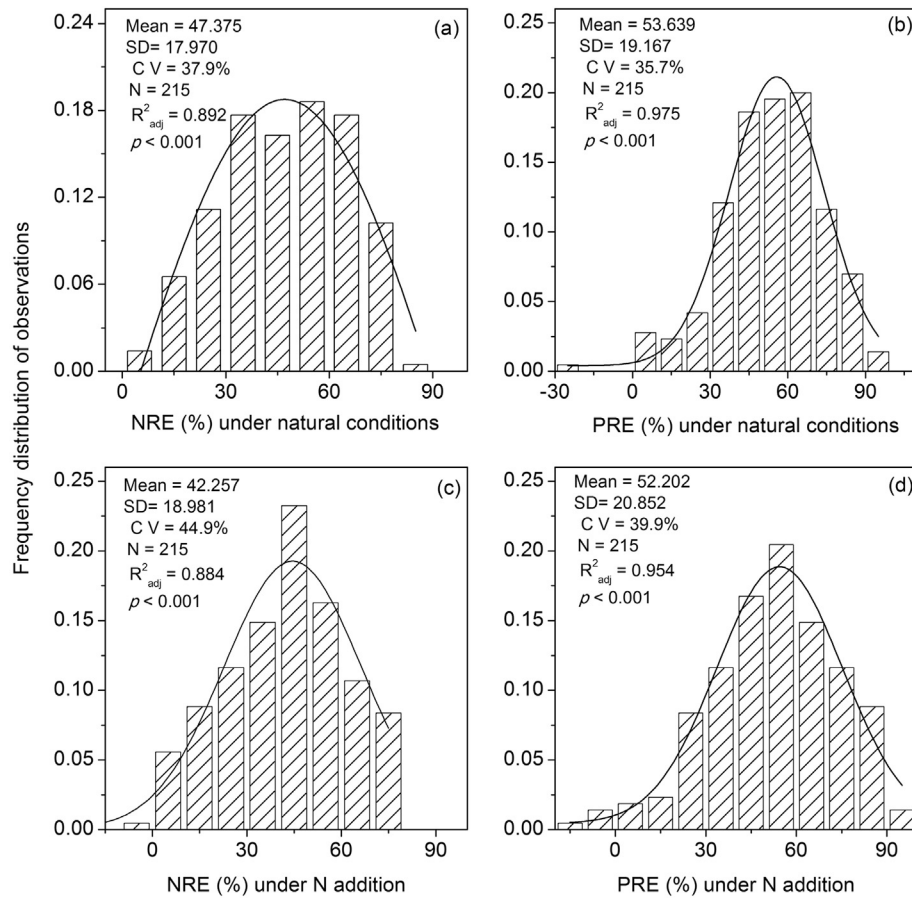
Fig. 2. Frequency distribution of the change in nitrogen resorption efficiency (NRE) (a) and phosphorus resorption efficiency (PRE) (b) under natural conditions; and the change in NRE (c) and PRE (d) under N addition on a global scale. The curves were fitted by a Gaussian function.

relatively lower than those in the control treatments (Fig. 5). These results indicate that N addition may weaken the relationship between N and P concentrations in green leaves. In addition, the N and P concentrations of senesced leaves were significantly related in the control treatment based on the regression models, and their R^2_{adj} values were

0.438 under N limitation, 0.575 under N and P-co-limitation, and 0.349 under P limitation (all $p < 0.001$, Fig. 6a, b, c). When the N and P concentrations in the senesced leaves in the N addition treatments were considered, the tendency of the change in the N and P relationship was similar to that in the control treatments (Fig. 6); the P
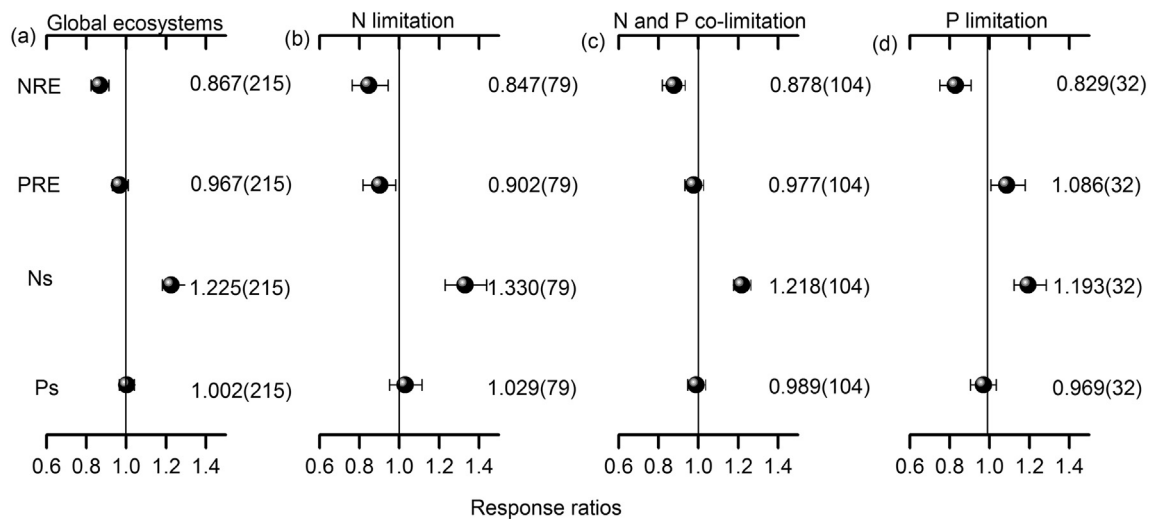
Fig. 3. Effects of nitrogen (N) addition on the nitrogen resorption efficiency (NRE), phosphorus (P) resorption efficiency (PRE), N and P concentrations in senesced leaves (Ns and Ps, respectively) of all plants global ecosystems (a), N limitation (b), N and P co-limitation (c) and P limitation (d). The numbers outside and inside the parentheses stand for the number of sample observations and the response ratio (RR), respectively. The dots with error bars indicate the mean effect size and the 95% confidence interval (95% CI).

Table 1

Comparison of the effects of nitrogen (N) addition on N resorption efficiency (NRE), phosphorus (P) resorption efficiency (PRE), and N and P concentrations in senesced leaves (Ns and Ps, respectively) under different nutrient-limited conditions (including N limitation, N and P-co-limitation and P limitation). Effect sizes represent the mean of the effects of N addition on the variable, and 95% CI indicates the 95% confidence interval. The heterogeneity between (Qb) is significant at $p < 0.05$, which indicates that the response ratios (RRs) of the variables differ among different nutrient-limited conditions.

Nutrient limitation	NRE				PRE			
	Effect size	95%CI		Qb	Effect size	95%CI		Qb
N limitation	0.847	0.765	0.935	0.728	0.902	0.818	0.982	**< 0.001**
N and P co-limitation	0.878	0.819	0.929		0.977	0.929	1.022	
P limitation	0.829	0.752	0.908		1.086	1.005	1.179	
Nutrient limitation	Ns				Ps			
	Effect size	95%CI		Qb	Effect size	95%CI		Qb
N limitation	1.330	1.229	1.438	**0.040**	1.029	0.951	1.114	0.342
N and P co-limitation	1.218	1.177	1.263		0.988	0.948	1.038	
P limitation	1.193	1.123	1.284		0.969	0.904	1.033	

Bold values indicate that the effects of the treatment on the measured parameters are significant.

concentration increased with increasing N concentrations under N limitation, N and P-co-limitation, and P limitation ($R^2_{adj} = 0.394$, 0.728, 0.316; all $p < 0.001$, Fig. 6a, b, c).

To quantify the effects of N addition on the relationship between N and P concentrations in green and senesced leaves under different nutrient-limited conditions, we compared the coefficients and the intercepts of the relationships based on the regression models. The coefficients and intercepts in the regression models of N and P concentrations in green leaves in the control treatments and those in the N addition treatments differed significantly (all with $p < 0.05$, expect for one value of 0.567, Table 2). However, the coefficients and intercepts in the regression models of N and P concentrations in senesced leaves did not differ significantly between the control and the N addition treatments (all with $p > 0.05$, except for one value of 0.039, Table 2). These results suggest that N addition significantly changed the relationship between N and P concentrations in green leaves but only slightly affected the relationship in senesced leaves under each nutrient-limited condition.

4. Discussion

4.1. Estimating global NRE and PRE and characterizing their variables

Our results showed that the global mean NRE and PRE values for all plant groups were approximately 47.4% and 53.6%, respectively, under natural conditions (Fig. 4), and comparable to estimates from global-scale syntheses. These findings from previous studies have shown that the global average range of NRE and PRE among plant functional groups was approximately 46.9% to 62.1% and 52% to 64.9% under natural conditions, respectively (Aerts, 1996; Vergutz et al., 2012; Yuan and Chen, 2009). However, the coefficient of variation of NRE and PRE under natural conditions was greatly variable on a global scale in this study, which is consistent with previous studies (Vergutz et al., 2012; Wright and Westoby, 2003; Yuan and Chen, 2009). Several factors may explain this phenomenon. First, the high variability of NRE and PRE may be modulated by geographical and climatic factors. For example, our
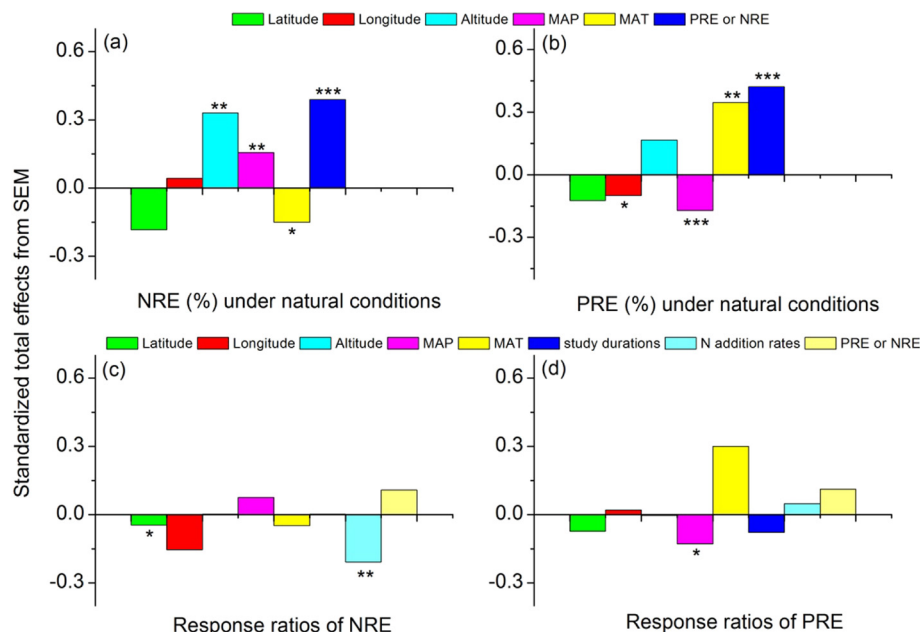

Fig. 4. Standardized total effect (including the direct and indirect effects) of geography (latitude, longitude and altitude) and climatic (mean annual temperature (MAT) and mean annual precipitation (MAP)) factors or experimental parameters (study durations and nitrogen (N) addition rates) on the global variations in nitrogen resorption efficiency under natural conditions or on the response ratios of nitrogen resorption efficiency to N addition. a, nitrogen resorption efficiency (NRE); b, phosphorus resorption efficiency (PRE); c, the response ratios (RRs) of NRE to N addition; d, the response ratios (RRs) of PRE to N addition. The model satisfactorily fit the data based on the χ^2, NFI, CFI and RMSEA values ($\chi^2 = 9.580$, df = 3, NFI = 0.980, CFI = 0.985 and RMSEA = 0.101 in (a) and (b); $\chi^2 = 9.419$, df = 3, NFI = 0.980, CFI = 0.985 and RMSEA = 0.100 in (c) and (d)). *, **, and *** indicate significant direct effects of drivers on target variables at the $p < 0.1$, $p < 0.01$, and $p < 0.001$ levels, respectively.
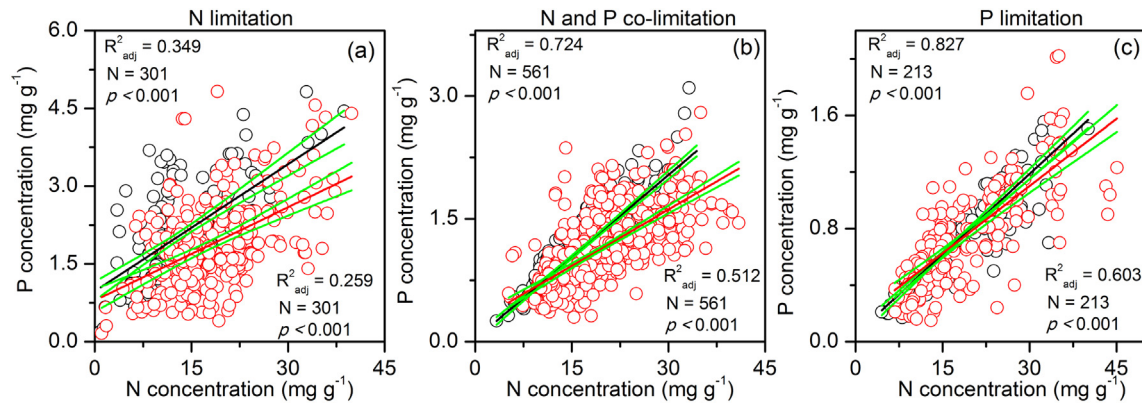
Fig. 5. Relationships between nitrogen (N) and phosphorus (P) concentrations in green leaves under different nutrient-limited conditions. a, N limitation; b, N and P co-limitation; c, P limitation. The solid lines were plotted to determine significant relationships at a confidence level of $p < 0.05$. Black hollow circles and equations in the upper left corner refer to natural conditions, and red hollow circles and equations in the lower right corner refer to N addition. The green lines represent the fitted lines of the 95% confidence interval (95% CI).

results showed that altitude and MAP directly and positively influenced the NRE, which was directly and negatively influenced by MAT (Fig. 4a). In contrast, the PRE under natural conditions was directly and primarily regulated by MAT, MAP and longitude (Fig. 4a). Yuan and Chen (2009) also found that latitude, MAT and MAP could explain 25%, 20% and 23% of the variability in NRE and 26%, 16% and 7% of the variability in PRE, respectively. Second, the results in this study demonstrated that NRE and PRE were positively correlated under natural conditions, which is consistent with the previous studies (Han et al., 2013; Lü et al., 2016) and indicates that a synergism between NRE and PRE. Therefore, nutrient resorption efficiency may be regulated by the relative limitations of N and P (Han et al., 2013). Third, plant growth forms, such as woody plants vs. herbaceous plants, coniferous plants vs. broadleaf plants, and graminoids vs. forbs, and species specificity may profoundly impact the variability in nutrient resorption efficiency (Fig. S5 in the Supporting Information) (Aerts, 1996; Huang et al., 2018; Vergutz et al., 2012; Yuan and Chen, 2009). Fourth, leaf characteristics such as leaf lifespan (Cordell et al., 2001; Wright and Westoby, 2003), leaf shape (Yuan and Chen, 2009), leaf mass (Heerwaarden et al., 2003; Lmvan et al., 2003), leaf area (Heerwaarden et al., 2003) and leaf nutrient contents (Huang et al., 2007; Kobe et al., 2005) may significantly influence nutrient resorption efficiency. Therefore, these findings suggest that the general pattern of nutrient resorption under natural conditions is run by geographical and climatic factors and also can be regulated by the pattern of nutrient limitation and plant characteristics.

Our results also showed that N addition significantly decreased the NRE by 13.3% but slightly affected the PRE on a global scale, which is consistent with a previous study (Yuan and Chen, 2015a). Yuan and Chen (2015a) reported that N addition significantly decreased the mean NRE for all plant growth types by approximately 12.2% but did not affect the PRE on a global scale. However, Aerts and Chapin III (1999) hypothesized that soil nutrient conditions would significantly affect nutrient resorption, but these conditions have remained highly controversial in subsequent studies (Vergutz et al., 2012; Wright and Westoby, 2003; Yuan and Chen, 2015a). Here, two parallel lines of evidence from our study support this hypothesis. First, the results showed that N addition remarkably decreased the NRE under all nutrient-limited conditions (Table 1), which is similar to previous studies (Lü et al., 2016; Mao et al., 2013; Yuan and Chen, 2015a). Second, the responses of PRE to N addition can be regulated by different nutrient limitations, and negative, positive, and neutral effects on the PRE were found under N-limited, P-limited, and N and P-co-limited conditions, respectively (Fig. 5). Two mechanisms likely led to these phenomena. First, different soil nutrient regimes can result in different nutrient use strategies in plants. For example, plants from infertile soils usually adopt a "conservative consumption" nutrient use strategy and have high nutrient resorption efficiency to ensure their survival and reproduction (Aerts and Chapin III, 1999; Wright and Cannon, 2001). In contrast, plants from nutrient-rich fields prefer to absorb nutrients from the soil and thus usually exhibit low nutrient resorption efficiency and
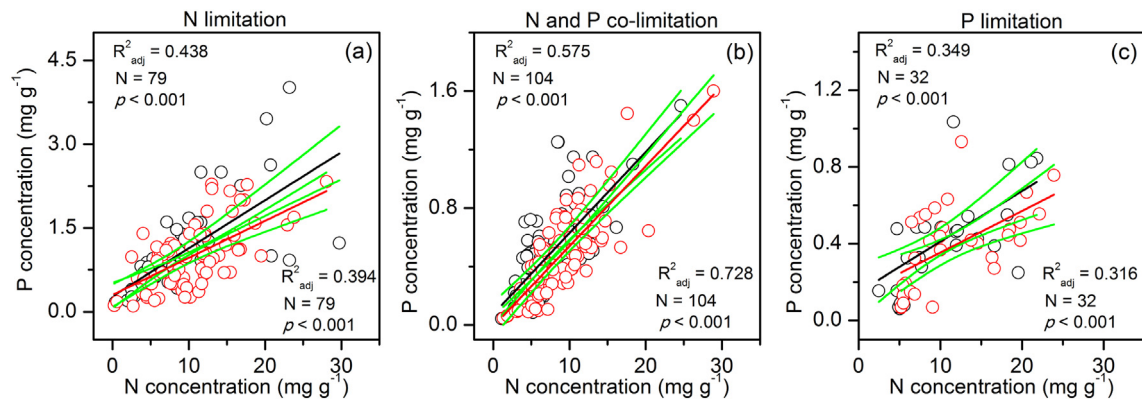
Fig. 6. Relationships between nitrogen (N) and phosphorus (P) concentrations in senesced leaves under different nutrient-limited conditions. a, N limitation; b, N and P co-limitation; c, P limitation. The solid lines were plotted to determine significant relationships at a confidence level of $p < 0.05$. Black hollow circles and equations in the upper left corner refer to natural conditions, and red hollow circles and equations in the lower right corner refer to N addition. The green lines represent the fitted lines of the 95% confidence interval (95% CI).

Table 2
Comparison of the coefficients and intercepts between the regression equations of nitrogen (N) and phosphorus (P) under natural conditions (the control treatment) and under N addition in green and senesced leaves under different nutrient-limited conditions based on general linear models.

Nutrient limitation	Treatment	Equation	N	R^2_{adj}	$F_{coefficient}$ (p)	$F_{intercept}$ (p)
Green-leaf						
N limitation	Control	y = 0.082x + 0.974	301	0.349	6.157 (**p = 0.013**)	76.975 (**p < 0.001**)
	N addition	y = 0.059x + 0.794	301	0.259		
N and P co-limitation	Control	y = 0.067x + 0.033	561	0.724	60.936 (**p < 0.001**)	77.751 (**p < 0.001**)
	N addition	y = 0.046x + 0.241	561	0.512		
P limitation	Control	y = 0.038x + 0.051	213	0.827	7.901 (**p = 0.005**)	0.328 (p = 0.567)
	N addition	y = 0.032x + 0.151	213	0.603		
Senesced-leaf						
N limitation	Control	y = 0.086x + 0.276	79	0.438	1.910 (p = 0.169)	4.325 (**p = 0.039**)
	N addition	y = 0.066x + 0.302	79	0.394		
N and P co-limitation	Control	y = 0.055x + 0.074	104	0.575	0.013 (p = 0.910)	2.416 (p = 0.122)
	N addition	y = 0.055x − 0.010	104	0.728		
P limitation	Control	y = 0.026x + 0147	32	0.349	0.312 (p = 0.578)	1.562 (p = 0.216)
	N addition	y = 0.022x + 0.136	32	0.316		

Bold values indicate significant differences between the coefficients or intercepts of the control treatment and N addition treatment in green and senesced leaves.

adopt a "resource spending" nutrient use strategy to grow and develop (Aerts and Chapin III, 1999; Wright and Cannon, 2001). It is well known that increasing N deposition may significantly improve soil N availability (Li et al., 2016; You et al., 2017), thus altering the nutrient use strategy of plants. The results of our study also indicated that the N addition rates can directly and negatively affect the response of NRE to N addition (Fig. 4c), which is supported by a previous study (Yuan and Chen, 2015a). Second, as discussed above, because N addition may significantly affect soil N and P availability (Fujita and Wassen, 2010; Li et al., 2016; Marklein and Houlton, 2012; You et al., 2017) and therefore change the relative limitation of N and P, plants will regulate their nutrient resorption efficiency and nutrient use efficiency to maintain a balance between N and P in their organs and tissues (Houlton et al., 2008). For example, under N limitation, N addition significantly increased soil N availability, thus decreasing the NRE (Lü et al., 2016; Mayor et al., 2014), whereas to maintain the balance with the NRE (Fig. S6 in the Supporting Information), the PRE will decrease accordingly as soil P availability is relatively high (Han et al., 2013; Reed et al., 2012). However, under P limitation, N addition can aggravate the limitation of P on plants (Li et al., 2016). Although excessive N addition may stimulate phosphate enzyme activities to increase soil P availability (Deng et al., 2016; Fujita and Wassen, 2010; Marklein and Houlton, 2012), plants can also increase their PRE to rapidly compensate for P deficiency (Fig. 3d) (Wang et al., 2014). Thus, these results indicate that nutrient regimes not only determine the nutrient use strategy but also regulate the response of the nutrient resorption efficiency in plants to global N deposition.

4.2. N and P concentrations in green and senesced leaves were significantly related to nutrient-limited conditions

Understanding the relationship between N and P in plants or ecosystems is critical for forecasting the response of plants or ecosystems to future environmental changes. The significant relationship between plant N and P has been demonstrated in different ecosystems, population, plant functional groups and organs in previous studies (He et al., 2008; Reich and Oleksyn, 2004; Yuan et al., 2011). The results from our study indicate that the relationships between N and P in green and senesced leaves were tightly coupled under different nutrient-limited conditions in natural ecosystems (Figs. 5, 6). These results could be attributed to the N in leaves being strongly linked to photosynthesis and plant growth (Walker et al., 2014), while P is important for genetic processing and supplying energy for plant metabolism (Borer et al., 2013; Elser et al., 2010; Reich et al., 2009). The coupled N and P relationship in green leaves can be used as an indicator to predict the stability of an individual in an ecosystem (Demars and Edwards, 2007), and the relationship in senesced leaves not only determines the nutrient

return but also directly regulates litter decomposition rates (Aerts et al., 2012). Therefore, these findings suggest that N and P are balanced in most parts of the ecosystem under natural conditions and play an important role in ecosystem function, energy flow and nutrient cycling. Unfortunately, we cannot determine whether the N and P relationships in green and senesced leaves vary significantly under different nutrient-limited conditions because the data from this study are limited in terms of statistical power.

4.3. The role of nutrient resorption in regulating the N and P relationship in senesced leaves under N addition

One of the objectives of our study was to identify how the relationships between N and P in green and senesced leaves are affected by N addition. Previous studies have shown that global change can cause the N and P cycles in plants and soil to become unbalanced or decoupled during biogeochemical cycling (Delgado-Baquerizo et al., 2013; Peñuelas et al., 2015; Wardle, 2013; Yuan and Chen, 2015b; Zhang et al., 2013). In this study, we found that N addition significantly weakened the relationship between N and P in green leaves but slightly affected the relationship in senesced leaves under nutrient-limited conditions (Table. 2, Figs. 5, 6). These results are similar to those from a case study, reporting that N and P were not related in green leaves and closely related in senesced leaves in response to nutrient enrichment (Lü et al., 2016). The relationship between N and P was weakened by N addition, mainly because N addition changes the N and P concentrations in green leaves. Previous studies have demonstrated that N addition can significantly increase the N concentration in green-leaves (Lü et al., 2016; Mao et al., 2013; Yuan and Chen, 2015a), and positive (Jones and Power, 2012; Lü et al., 2013), negative (Deng et al., 2017; Sardans et al., 2016) or neutral (Chen et al., 2015; Yuan and Chen, 2015a) effects on the P concentration in green leaves have been observed across ecosystems globally. As discussed above, this decoupling of N and P could decrease the stability of the individual in an ecosystem (Demars and Edwards, 2007) and alter N and P cycles (Yuan and Chen, 2015a), which leading to degenerative feedback between the plant and ecosystem (Sistla and Schimel, 2012). However, why did N addition not have a significant effect on the relationship between N and P in senesced leaves? In addition to a small amount of mass loss and elemental leaching (Duchesne et al., 2001; Heerwaarden et al., 2003), nutrient resorption primarily occurs during leaf senescence (Aerts, 1996; Vergutz et al., 2012; Yuan and Chen, 2015a). Through this process, plants can reabsorb nutrients from fresh litter to reuse the nutrients and reduce their dependence on soil nutrients (Aerts and Chapin III, 1999; Vergutz et al., 2012; Yuan and Chen, 2009). The results showed that N addition markedly decreased the NRE under all nutrient-limited conditions, and negative, positive and neutral effects on the PRE were found under N

limitation, P limitation and N and P co-limitation, respectively (Fig. 3b, c, d). However, we also found that plants under N addition can reabsorb more N and P from fresh litter than under natural conditions (Fig. S7 in the Supporting Information). These results indicate that nutrient resorption can reduce the effects of N addition on N and P concentrations in senesced leaves and thus plays an important role in regulating the N and P relationship in senesced leaves, which is also supported by a previous study (Lü et al., 2016). Therefore, nutrient resorption is not only the survival mechanism by which plants adapt to barren soil (Wang et al., 2014) but it can also alter the nutrient dynamics in plants and soil (Aerts et al., 2012).

As discussed above, our results fully demonstrated that the relationship between N and P in senesced leaves was modulated by the effects of N addition on nutrient resorption. In addition, the results also further showed that the magnitude of the effect of N addition on NRE under different nutrient-limited conditions was relatively greater than that on PRE (Fig. 5). This phenomenon can be attributed to N enrichment, which mainly increased the available N concentration rather than the P concentration in the soil (Kou et al., 2016; Lü et al., 2016; You et al., 2017). This result suggests that NRE plays a dominant role in the response of the N and P relationship in senesced leaves to N addition and further implies that the addition of N affects N dynamics more than P dynamics under different nutrient-limited conditions. Furthermore, across the different nutrient-limited conditions, the change in the nutrient resorption pattern in response to N addition may cause different and complicated variations in the patterns of N and P concentrations in green and senesced leaves (Figs. 2, S7 in the Supporting Information). These findings indicate that the response of nutrient resorption patterns to N enrichment under different nutrient-limited conditions is more important for plant and nutrient cycles than previously thought. Therefore, global biogeochemical models must take into account the response of nutrient elements to global changes under different nutrient constraints when predicting the processes of biogeochemical cycles.

5. Conclusions

This meta-analysis is one of the first to estimate the response of nutrient resorption to N addition under different nutrient-limited conditions and to identify the role of nutrient resorption in regulating the response of the relationship between N and P to N enrichment on a global scale. The global mean NRE and PRE values under natural conditions were 47.4% and 53.6%, respectively, and these values were significantly regulated by geographical and climatic factors and plant characteristics. N addition significantly decreased the NRE by 13.3% but did not clearly affect the PRE on a global scale, and N addition rates and latitude negatively affected the effects of N addition on the NRE. Additionally, the responses of nutrient resorption to N addition differed across different nutrient-limited conditions, suggesting that nutrient regimes not only determine the nutrient use strategy but also regulate the response of nutrient resorption efficiency in plants to global N deposition. Moreover, N addition significantly weakened the relationship between N and P concentrations in green leaves but slightly affected the relationship in senesced leaves, so we conclude that the stoichiometry of N and P in senesced leaves shows high homeostasis under N deposition. Our results also revealed that the relationship between N and P in plant leaves was modulated by the effects of N addition on nutrient resorption efficiency, especially the NRE. These findings highlight the importance of nutrient-limited conditions in the nutrient resorption response to N addition and the magnitude of the role of nutrient resorption in regulating the stoichiometric relationship between N and P under N deposition. However, different plants may have different optimal N to P ratios (Mellert, 2012), which contribute to errors in the results, but the findings provide a new insight into how plants adopt to environmental changes across different nutrient-limited conditions.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2018.07.186.

References

Aerts, R., 1996. Nutrient resorption from senescing leaves of perennials: are there general patterns? J. Ecol. 84, 597–608.

Aerts, R., Chapin III, F.S.C., 1999. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. Adv. Ecol. Res. 30, 1–67.

Aerts, R., Bodegom, P.M.V., Cornelissen, J.H.C., 2012. Litter stoichiometric traits of plant species of high-latitude ecosystems show high responsiveness to global change without causing strong variation in litter decomposition. New Phytol. 196, 181.

An, D.S., Frenne, P.D., Ampoorter, E., Nevel, L.V., Demey, A., Wuyts, K., Verheyen, K., 2011. Cumulative nitrogen input drives species loss in terrestrial ecosystems. Glob. Ecol. Biogeogr. 20, 803–816.

Borer, E.T., Bracken, M.E.S., Seabloom, E.W., Smith, J.E., Cebrian, J., Cleland, E.E., Elser, J.J., Fagan, W.F., Gruner, D.S., Harpole, W.S., 2013. Global biogeography of autotroph chemistry: is insolation a driving force? Oikos 122, 1121–1130.

Chen, F.S., Niklas, K.J., Liu, Y., Fang, X.M., Wan, S.Z., Wang, H., 2015. Nitrogen and phosphorus additions alter nutrient dynamics but not resorption efficiencies of Chinese fir leaves and twigs differing in age. Tree Physiol. 35, 1106.

Cordell, S., Goldstein, G., Meinzer, F.C., Vitousek, P.M., 2001. Regulation of leaf life-span and nutrient-use efficiency of *Metrosideros polymorpha* trees at two extremes of a long chronosequence in Hawaii. Oecologia 127, 198.

Delgado-Baquerizo, M., Maestre, F.T., Gallardo, A., Bowker, M.A., Wallenstein, M.D., Quero, J.L., Ochoa, V., Gozalo, B., García-Gómez, M., Soliveres, S., 2013. Decoupling of soil nutrient cycles as a function of aridity in global drylands. Nature 502, 672–676.

Demars, B.O.L., Edwards, A.C., 2007. Tissue nutrient concentrations in freshwater aquatic macrophytes: high inter-taxon differences and low phenotypic response to nutrient supply. Freshw. Biol. 52, 2073–2086.

Deng, M., Liu, L., Sun, Z., Piao, S., Ma, Y., Chen, Y., Wang, J., Qiao, C., Wang, X., Li, P., 2016. Increased phosphate uptake but not resorption alleviates phosphorus deficiency induced by nitrogen deposition in temperate *Larix principis-rupprechtii* plantations. New Phytol. 212, 1019–1029.

Deng, Q., Hui, D., Dennis, S., Reddy, K.C., 2017. Responses of terrestrial ecosystem phosphorus cycling to nitrogen addition: a meta-analysis. Glob. Ecol. Biogeogr. 00, 1–16.

Duchesne, L., Ouimet, R., Camiré, C., Houle, D., 2001. Seasonal nutrient transfers by foliar resorption, leaching, and litter fall in a northern hardwood forest at Lake Clair Watershed, Quebec, Canada. Can. J. For. Res. 31, 333–344.

Durán, J., Morse, J.L., Groffman, P.M., Campbell, J.L., Christenson, L.M., Driscoll, C.T., Fahey, T.J., Fisk, M.C., Mitchell, M.J., Templer, P.H., 2015. Winter climate change affects growing-season soil microbial biomass and activity in northern hardwood forests. Glob. Chang. Biol. 20, 3568–3577.

Elser, J.J., Bracken, M.E., Cleland, E.E., Gruner, D.S., Harpole, W.S., Hillebrand, H., Ngai, J.T., Seabloom, E.W., Shurin, J.B., Smith, J.E., 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecol. Lett. 10, 1135.

Elser, J.J., Fagan, W.F., Kerkhoff, A.J., Swenson, N.G., Enquist, B.J., 2010. Biological stoichiometry of plant production: metabolism, scaling and ecological response to global change. New Phytol. 186, 593–608.

Finzi, A.C., Austin, A.T., Cleland, E.E., Frey, S.D., Houlton, B.Z., Wallenstein, M.D., 2011. Responses and feedbacks of coupled biogeochemical cycles to climate change: examples from terrestrial ecosystems. Front. Ecol. Environ. 9, 61–67.

Fujita, Y., Wassen, M.J., 2010. Increased N affects P uptake of eight grassland species: the role of root surface phosphatase activity. Oikos 119, 1665–1673.

Grime, J.P., 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. J. Ecol. 86, 902–910.

Güsewell, S., Koerselman, W., 2002. Variation in nitrogen and phosphorus concentrations of wetland plants. Perspect. Plant Ecol. 5, 37–61.

Güsewell, S., Koerselman, W., Verhoeven, J.T.A., 2003. Biomass N:P ratios as indicators of nutrient limitation for plant populations in wetlands. Ecol. Appl. 13, 372–384.

Han, W., Tang, L., Chen, Y., Fang, J., 2013. Relationship between the relative limitation and resorption efficiency of nitrogen vs phosphorus in woody plants. PLoS One 8, e83366.

Harpole, W.S., Ngai, J.T., Cleland, E.E., Seabloom, E.W., Borer, E.T., Bracken, M.E., Elser, J.J., Gruner, D.S., Hillebrand, H., Shurin, J.B., Smith, J.E., 2011. Nutrient co-limitation of primary producer communities. Ecol. Lett. 14, 852–862.

He, J.S., Wang, L., Flynn, D.F., Wang, X., Ma, W., Fang, J., 2008. Leaf nitrogen:phosphorus stoichiometry across Chinese grassland biomes. Oecologia 155, 301–310.

Hedges, L.V., Gurevitch, J., Curtis, P.S., 1999. The meta-analysis of response ratios in experimental ecology. Ecology 80, 1150–1156.

Heerwaarden, L.M.V., Toet, S., Aerts, R., 2003. Current measures of nutrient resorption efficiency lead to a substantial underestimation of real resorption efficiency: facts and solutions. Oikos 101, 664–669.

Houlton, B.Z., Wang, Y.P., Vitousek, P.M., Field, C.B., 2008. A unifying framework for dinitrogen fixation in the terrestrial biosphere. Nature 454, 327.

Huang, J., Wang, X., Yan, E., 2007. Leaf nutrient concentration, nutrient resorption and litter decomposition in an evergreen broad-leaved forest in eastern China. For. Ecol. Manag. 239, 150–158.

Huang, G., Su, Y.G., Mu, X.H., Li, Y., 2018. Foliar nutrient resorption responses of three life-form plants to water and nitrogen additions in a temperate desert. Plant Soil 424, 1–11.

Jones, A.G., Power, S.A., 2012. Field-scale evaluation of effects of nitrogen deposition on the functioning of heathland ecosystems. J. Ecol. 100, 331–342.

Killingbeck, K.T., 1996. Nutrients in senesced leaves: keys to the search for potential resorption and resorption proficiency. Ecology 77, 1716–1727.

Kobe, R.K., Lepczyk, C.A., Iyer, M., 2005. Resorption efficiency decreases with increasing green leaf nutrients in a global data set. Ecology 86, 2780–2792.

Koricheva, J., Gurevitch, J., 2014. Uses and misuses of meta-analysis in plant ecology. J. Ecol. 102, 828–844.

Kou, L., Wang, H., Gao, W., Chen, W., Yang, H., Li, S., 2016. Nitrogen addition regulates tradeoff between root capture and foliar resorption of nitrogen and phosphorus in a subtropical pine plantation. Trees 1–15.

Kozovits, A.R., Mmc, B., Garofalo, C.R., Bucci, S., Franco, A.C., Goldstein, G., Meinzer, F.C., 2007. Nutrient resorption and patterns of litter production and decomposition in a Neotropical Savanna. Funct. Ecol. 21, 1034–1043.

Lebauer, D.S., Treseder, K.K., 2008. Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. Ecology 89, 371–379.

Li, Y., Niu, S., Yu, G., 2016. Aggravated phosphorus limitation on biomass production under increasing nitrogen loading: a meta-analysis. Glob. Chang. Biol. 22, 934.

Lmvan, H., Toet, S., Aerts, R., 2003. Nitrogen and phosphorus resorption efficiency and proficiency in six-arctic bog species after 4 years of nitrogen fertilization. J. Ecol. 91, 1060–1070.

Lü, X.T., Han, X.G., 2010. Nutrient resorption responses to water and nitrogen amendment in semi-arid grassland of Inner Mongolia, China. Plant Soil 327, 481–491.

Lü, X.T., Reed, S., Yu, Q., He, N.P., Wang, Z.W., Han, X.G., 2013. Convergent responses of nitrogen and phosphorus resorption to nitrogen inputs in a semiarid grassland. Glob. Chang. Biol. 19, 2775–2784.

Lü, X.T., Reed, S.C., Yu, Q., Han, X.G., 2016. Nutrient resorption helps drive intra-specific coupling of foliar nitrogen and phosphorus under nutrient-enriched conditions. Plant Soil 398, 1–10.

Mao, R., Song, C.C., Zhang, X.H., Wang, X.W., Zhang, Z.H., 2013. Response of leaf, sheath and stem nutrient resorption to 7 years of N addition in freshwater wetland of Northeast China. Plant Soil 364, 385–394.

Marklein, A.R., Houlton, B.Z., 2012. Nitrogen inputs accelerate phosphorus cycling rates across a wide variety of terrestrial ecosystems. New Phytol. 193, 696.

Mayor, J.R., Wright, S.J., Turner, B.L., 2014. Species-specific responses of foliar nutrients to long-term nitrogen and phosphorus additions in a lowland tropical forest. J. Ecol. 102, 36–44.

Mellert, K.H., 2012. Comparison of new foliar nutrient thresholds derived from van den Burg's literature compilation with established central European references. Eur. J. For. Res. 131, 1461–1472.

Moher, D., Liberati, A., Tetzlaff, J., Altman, D.G., Group, P, 2009. Preferred reporting items for systematic reviews and meta-analyses: the PRISMA statement. Rev. Esp. Nutr. Hum. Diet. 18, 889–896.

Niu, S., Classen, A.T., Dukes, J.S., Kardol, P., Liu, L., Luo, Y., Rustad, L., Sun, J., Tang, J., Templer, P.H., 2016. Global patterns and substrate-based mechanisms of the terrestrial nitrogen cycle. Ecol. Lett. 19, 697.

Peñuelas, J., Poulter, B., Sardans, J., Ciais, P., van der Velde, M., Bopp, L., Boucher, O., Godderis, Y., Hinsinger, P., Llusia, J., 2013. Human-induced nitrogen-phosphorus imbalances alter natural and managed ecosystems across the globe. Nat. Commun. 4, 2934.

Peñuelas, J., Sardans, J., Rivas-Ubach, A., Janssens, I.A., 2015. The human-induced imbalance between C, N and P in Earth's life system. Glob. Chang. Biol. 18, 3–6.

Reed, S.C., Townsend, A.R., Davidson, E.A., Cleveland, C.C., 2012. Stoichiometric patterns in foliar nutrient resorption across multiple scales. New Phytol. 196, 173–180.

Reich, P.B., Oleksyn, J., 2004. Global patterns of plant leaf N and P in relation to temperature and latitude. Proc. Natl. Acad. Sci. U.S.A 101, 11001.

Reich, P.B., Oleksyn, J., Wright, I.J., 2009. Leaf phosphorus influences the photosynthesis-nitrogen relation: a cross-biome analysis of 314 species. Oecologia 160, 207–212.

Rejmánková, E., 2005. Nutrient resorption in wetland macrophytes: comparison across several regions of different nutrient status. New Phytol. 167, 471–482.

Rejmánková, E., Snyder, J.M., 2008. Emergent macrophytes in phosphorus limited marshes: do phosphorus usage strategies change after nutrient addition? Plant Soil 313, 141–153.

Sardans, J., Alonso, R., Janssens, I.A., Carnicer, J., Vereseglou, S., Rillig, M.C., Fernández-Martínez, M., Sanders, T.G.M., Peñuelas, J., 2016. Foliar and soil concentrations and stoichiometry of nitrogen and phosphorous across European Pinus sylvestris forests: relationships with climate, N deposition and tree growth. Funct. Ecol. 30, 676–689.

Sistla, S.A., Schimel, J.P., 2012. Stoichiometric flexibility as a regulator of carbon and nutrient cycling in terrestrial ecosystems under change. New Phytol. 196, 68.

Tessier, J.T., Raynal, D.J., 2003. Use of nitrogen to phosphorus ratios in plant tissue as an indicator of nutrient limitation and nitrogen saturation. J. Appl. Ecol. 40, 523–534.

Vergutz, L., Manzoni, S., Porporato, A., Novais, R.F., Jackson, R.B., 2012. Global resorption efficiencies and concentrations of carbon and nutrients in leaves of terrestrial plants. Ecol. Monogr. 82, 205–220.

Vitousek, P.M., Porder, S., Houlton, B.Z., Chadwick, O.A., 2010. Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen-phosphorus interactions. Ecol. Appl. 20, 5.

Walker, A.P., Beckerman, A.P., Gu, L., Kattge, J., Cernusak, L.A., Domingues, T.F., Scales, J.C., Wohlfahrt, G., Wullschleger, S.D., Woodward, F.I., 2014. The relationship of leaf photosynthetic traits-Vcmax and Jmax-to leaf nitrogen, leaf phosphorus, and specific leaf area: a meta-analysis and modeling study. Ecol. Evol. 4, 3218.

Wang, M., Murphy, M.T., Moore, T.R., 2014. Nutrient resorption of two evergreen shrubs in response to long-term fertilization in a bog. Oecologia 174, 365.

Wardle, D.A., 2013. Ecology: drivers of decoupling in drylands. Nature 502, 628–629.

Wright, I.J., Cannon, K., 2001. Relationships between leaf lifespan and structural defences in a low-nutrient, sclerophyll flora. Funct. Ecol. 15, 351–359.

Wright, I.J., Westoby, M., 2003. Nutrient concentration, resorption and lifespan: leaf traits of Australian sclerophyll species. Funct. Ecol. 17, 10–19.

Xu, S., Zhou, G., Tang, X., Wang, W., Wang, G., Ma, K., Han, S., Du, S., Li, S., Yan, J., 2017. Different spatial patterns of nitrogen and phosphorus resorption efficiencies in China's forests. Sci. Rep. 7.

Yan, Z., Kim, N., Han, W., Guo, Y., Han, T., Du, E., Fang, J., 2015. Effects of nitrogen and phosphorus supply on growth rate, leaf stoichiometry, and nutrient resorption of Arabidopsis thaliana. Plant Soil 388, 147–155.

You, C., Wu, F., Gan, Y., Yang, W., Hu, Z., Xu, Z., Tan, B., Liu, L., Ni, X., 2017. Grass and forbs respond differently to nitrogen addition: a meta-analysis of global grassland ecosystems. Sci. Rep. 7, 1563.

Yuan, Z.Y., Chen, H.Y.H., 2009. Global-scale patterns of nutrient resorption associated with latitude, temperature and precipitation. Glob. Ecol. Biogeogr. 18, 11–18.

Yuan, Z.Y., Chen, H.Y., 2015a. Negative effects of fertilization on plant nutrient resorption. Ecology 96, 373.

Yuan, Z.Y., Chen, H.Y.H., 2015b. Decoupling of nitrogen and phosphorus in terrestrial plants associated with global changes. Nat. Clim. Chang. 5, 465–469.

Yuan, Z.Y., Chen, H.Y.H., Reich, P.B., 2011. Global-scale latitudinal patterns of plant fine-root nitrogen and phosphorus. Nat. Commun. 2, 344.

Yue, K., Peng, Y., Peng, C., Yang, W., Peng, X., Wu, F., 2016. Stimulation of terrestrial ecosystem carbon storage by nitrogen addition: a meta-analysis. Sci. Rep. 6.

Yue, K., Fornara, D.A., Yang, W., Peng, Y., Li, Z., Wu, F., Peng, C., 2017. Effects of three global change drivers on terrestrial C:N:P stoichiometry: a global synthesis. Glob. Chang. Biol. 23, 2450.

Yue, K., García-Palacios, P., Parsons, S.A., Yang, W., Peng, Y., Tan, B., Huang, C., Wu, F., 2018. Assessing the temporal dynamics of aquatic and terrestrial litter decomposition in an alpine forest. Funct. Ecol. https://doi.org/10.1111/1365-2435.13143.

Zhang, N., Guo, R., Song, P., Guo, J., Gao, Y., 2013. Effects of warming and nitrogen deposition on the coupling mechanism between soil nitrogen and phosphorus in Songnen Meadow Steppe, northeastern China. Soil Biol. Biochem. 65, 96–104.